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## The respiratory system of the Carolina locust (*Dissosteira carolina* Linn.)

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THE RESPIRATORY SYSTEM OF THE CAROLINA LOCUST

(Dissosteira carolina Linne)

By Stuart C. Vinal, B. Sc.

Thesis submitted for the degree of Master of Science

Massachusetts Agricultural College

Amherst, Massachusetts

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# THE RESPIRATORY SYSTEM OF THE CAROLINA LOCUST\*

(Dissosteira carolina Linne)

By Stuart C. Vinal, B. Sc.

The present paper, which is offered as a portion of a thesis for the degree of Master of Science at the Massachusetts Agricultural College, is one of a series of studies being conducted at this institution on the anatomy of the Carolina locust for the purpose of furnishing a description of the morphology of a common and widely distributed insect which is both primitive in its organization and of sufficient size to be readily dissected. In the preparation of this paper I have received much encouragement and assistance from Dr. H. T. Fernald, Dr. G. C. Crampton, and Dr. W. S. Regan, and I would take this opportunity of expressing my appreciation of their kindly interest and advice.

\*Contribution from the Entomological Laboratory of the Massachusetts Agricultural College, Amherst, Mass.



### Historical

Aristotle (about 320 B. C.) propounded the theory that insects did not breathe, and it was not until the time of Malpighi (1669) that it was demonstrated that insects respire by means of internal tracheae. The studies of Malpighi (1669) on the silk worm, of Swammerdam (1673) on the honey bee, and of Lyonet (1762) on the goat moth paved the way for later investigations, but the famous monograph of Straus-Durckheim (1828) on the anatomy of the cockchafer (Melolontha vulgaris L.) in which the tracheal system is treated in great detail, furnishes the basis for all modern work on the subject, such as that of Alt (1912) on the respiratory system of Dytiscus marginalis L., etc.

Among the works dealing with the respiratory system of Orthoptera in particular, may be mentioned the investigations of Marcel de Serres (1819) on Truxalis nasutus, Leon Dufour (1841) on the Anatomy of the Orthoptera, Hymenoptera and Neuroptera, and Miall and Denny (1886) on the cockroach. Minot (1877-1879) has given an excellent general description of the tracheal system of the red legged locust (Melanoplus femurrubrum DeG.) but his work is lacking in detail, and contains many inaccuracies, due no doubt to the fact that the dissecting microscopes available at that time were but crude implements in comparison with the perfected binoculars of today and even with the help of our improved appliances and technique, the tracing out of the various ramifications of the tracheal system requires much time and patience. Snodgrass (1903) has apparently described the general features of the tracheal system in Dissosteira, but his paper is not accessible to me and but few copies of it were ever printed. Therefore, since no detailed account of the respiratory system of any primitive insect is at present available in this





connection, the morphology of the tracheal system of Dissosteira has been worked out in the present paper, to fill this lack.



## Organs of Respiration

### A. External Organs or Spiracles (Plate I; Fig. 4.)

Ten pairs of spiracles are present in *Dissostertia carolina*, two pairs of which are located on the sides of the thorax and eight pairs on the abdomen.

#### I. Situation (Plate I, Fig. 4.)

The first thoracic spiracle (I) lies in the lateral inter-segmental membranous region connecting the pro- and meso-thorax, and beneath the hind lobe of the pronotum.

The second thoracic spiracle (II) is situated just above the second coxal cavity between the meso- and meta-thorax.

The first abdominal spiracle (III) lies in the auditory cavity just anterior to the tympanal sense organ. The other seven pairs of abdominal spiracles (IV to X) are all similarly placed on the lower anterior margin of each dorsal plate to the ninth abdominal segment where no spiracles are present.

#### II. Morphology

In the Carolina locust three types of spiracles are found.

a. First Thoracic Spiracle (Plate II, Fig. 11.). This is by far the largest spiracle in the body and is closed externally by a large two lobed valve. The basal portion of the anterior lobe is prolonged somewhat posteriorly and is a protruded portion of the body wall. The aperture immediately within the valve is divided into two chambers, each of which leads to a separate main tracheal tube. Between these tracheae is a chitinous septum (stm) which arises at the inner side of the posterior valvular lobe and extends anteriorly. Here it is thickened





on its free end to which an occlusor muscle (ocm) is attached. Two valvular muscles are connected to an internal chitinous projection which arises at the lower anterior corner of the forward lobe. One muscle is inserted at the thickened end of the septum (see Fig. 11) and is the true occlusor muscle, while the other runs to the outer edge of the posterior lobe. As mentioned above two separate main tracheal tubes arise directly from this spiracle as shown in figure 11. The dorsal or larger air tube furnishes the cephalic tracheae, while the lower or smaller air tube gives off its branches to the thoracic muscles.

b. Second Thoracic Spiracle (Plate II, Fig. 12). This consists of an external two lobed valve the anterior lobe of which is considerably larger than the posterior one, and leads directly into a single main tracheal tube. Each lobe is somewhat triangular in outline and their opposing corners are connected internally by a chitinous cross band. The occlusor muscle (ocm) is inserted at the middle of this band and extends ventrally to a chitinous projection of the integument. The contraction of this muscle draws both lobes together.

c. Abdominal Spiracles (Plate II, Fig. 13). These differ markedly from the thoracic spiracles, their external orifice being permanently open and leading directly into a shallow oval cup which communicates with a single main trachea. The occluding apparatus is quite different from those described above and consists of an internal hinged lobe at the apex of which the occlusor muscle (ocm) is attached. The abdominal spiracles are partly surrounded by a peculiar semicircular horny margin which is merely the infolded edge of the integument surrounding the spiracle. The occluding lobe (left lobe Fig. 13) is drawn down upon this horny margin by the occluding muscle (ocm) thus cutting off the supply of air to the tracheal tube.





Each of the eight pairs of abdominal spiracles is constructed on the above plan, the first and last merely differing from the others in their larger size.

### B. Tracheal System

It is necessary to make a large number of dissections in order to obtain an accurate knowledge of this complicated system, for it is impossible by a single dissection to show all the tracheae contained within the body.

In studying the tracheal system alcoholic specimens proved to be of very little value, as tracheae filled with this fluid can be traced only with great difficulty. An attempt was made to fill the tracheae with India ink, melted wax, and other substances, by submerging the insect in these materials and exhausting the air from the container, in the hope that atmospheric pressure would force these substances into the tracheae when the air was again admitted, but these proved unsatisfactory. It was found that tracheae containing air were very easily traced when dissected specimens were submerged in water, but this necessitated fresh insects.

After considerable experimentation the following method was devised for the preservation of locusts with air in their tracheae.

The Carolina locusts were caught and killed in a cyanide bottle in the usual manner. At the close of a collecting trip these insects were placed in a desiccator on a wire gauze, the bottom part of which was partly filled with 8% formalin solution. This proved to be very satisfactory in preserving the air in the tracheal system and preventing the insects from hardening while the formalin gas liberated prevented molds and <sup>bacteria</sup> ~~baeilli~~ from breaking down the insect tissue.





## I. Structure of the Tracheae

The tracheal system of insects originates in the embryo as tubular invaginations of the ectodermal layer, and therefore the fundamental structure is similar to that of the body wall. The tracheae are elastic tubes lined by a chitinous layer corresponding to the chitinous exoskeleton of an insect, and are surrounded by an epithelial layer continuous with that of the hypodermis. The inner chitinous lining, called the intima, is thickened at regular intervals to form spiral threads, called taenidia, which are not continuous throughout the tracheal tube but are frequently broken. The taenidia function in keeping the tracheae permanently open without affecting their flexibility. These elastic threads are not found in the ultimate branches of the tracheae, called tracheoles or in the air sacs.

## II. General Morphology of the Tracheal System

A detailed description of this system would require a very lengthy paper. It is therefore advisable to consider only the more important tracheae found in the Carolina locust in the present article.

The tracheal system of the grasshopper may be divided into three distinct parts

- (1) Cephalic tracheae
- (2) Thoracic tracheae
- (3) Abdominal tracheae

These will be treated separately in the following pages.



### a. Cephalic Tracheae

As we have seen, the first thoracic spiracle (Plate II, Fig. 11) is composed of two chambers which give rise to two tracheal tubes. The upper chamber or larger opening leads into a large main tube which soon divides forming two main tracheae which run to the head. The dorsal branch, termed the superior cephalic trachea (Plate I, Fig. 1, I<sub>1</sub>) runs to the dorsal surface of the head and joins the ophthalmic trachea (Plate I, Fig. 5; ot) surrounding the compound eye at the vertex (Plate II, Fig. 10). The second branch, known as the median cephalic trachea, soon divides and sends a branch to the external lateral head muscles (Plate I, Fig. 5; I<sub>2a</sub>). This also connects dorsally with the superior cephalic trachea and ventrally with the anterior tentorial arm plexus (Tp) as shown in Fig. 5. The other branch of the median cephalic trachea (Plate I, Fig. 1; I<sub>2b</sub>) passes through the occipital foramen with the alimentary canal and divides forming two branches at the main body of the tentorium. One branch (Fig. 1; I<sub>2b'</sub>) travels along the anterior edge of the dorsal tentorial arm giving off numerous small branches to the muscles and ends in a large air sac (A) situated over the alimentary canal (also see Plate II, Fig. 14). The second branch of I<sub>2b</sub> (Fig. 1, I<sub>2b''</sub>) extends forward and gives off a small branch closely applied to the proventriculus while the main tube runs to the under surface of the brain. Here it forms a large number of vesicular air sacs, which completely surround this organ. Just before the median cephalic trachea divides to form its two main tracheae running to the head a ventral branch is given off which unites with the inferior thoraco-cephalic trachea (Plate I, Fig. 1; tc). The thoraco-cephalic trachea (tc) enters the head just beneath the body of the tentorium, (see Fig. 1 & Fig. 14), then curves laterally giving off branches to the labium, maxillae, and





mandibles, while the main tube continues on and ends at the plexus situated at the junction of the anterior tentorial arm and external chitin (Fig. 5).

The following tubes constitute the more important tracheae found in the head region.

The ophthalmic trachea (Plate I, Fig. 5, ot) surrounding the compound eye gives off numerous branches which supply the optic ganglia. A large sac-like tube (gt) originates from the ventral portion of the ophthalmic trachea and runs ventrally beneath the gena to the anterior tentorial plexus (Tp) previously mentioned. Connecting these tentorial arm plexuses is a large transverse dilated trachea which passes in the front of the head just above the junction of the clypeus and frons (Fig. 5). From this tube, branches are given off to the clypeus and labrum. Medially this transverse tube gives off a dorsal dilated air sac which supplies the front of the head and connects dorsally with both the ophthalmic and superior cephalic tracheae.

All the above mentioned tracheae receive air through the large chamber of the first thoracic spiracle, with the exception of the thoraco-cephalic trachea which receives air from the first, second and third spiracles (I, II, III) in a more or less indirect manner.



### b. Thoracic Tracheal System

The thorax contains many muscles all of which must be intimately supplied with oxygen. This necessitates a large number of tracheae whose arrangement is very complicated. The tracing of this system becomes very difficult because upon removing a muscle to expose the tracheae beneath ~~it~~ a large number of the connections between the tracheal tubes of each layer are destroyed.

The tracheae situated in the median sagittal plane will be discussed first (Plate I, Fig. 1). The other figures (Fig. 2 and Fig. 3) are drawn looking from within and removing one muscle layer at a time until the last layer is reached which is drawn both from within (Fig. 3) and by removing the external chitin of the thorax (Plate II, Fig. 7)

In general, tracheal tubes originate at the lower or smaller chamber of the first thoracic spiracle and pass backward between the muscle layers to the first abdominal spiracle (III) and connect with the second spiracular plexus at the different intersections of this plexus and the muscle layers.

The tracheal system of the thorax is best understood if two divisions are discussed separately (1) Dorsal tracheae which supply air to most of the thoracic muscles and (2) Ventral tracheae which supply the head, nervous system and legs with tracheae.

Dorsal Thoracic<sup>c</sup> Tracheae. The median sagittal section and its air tubes will be discussed first (Plate 1, Fig. 1). From spiracle III a branch is given off which runs to the median surface of the dorso-longitudinal muscles (III-Ba) where it divides into three branches which distribute themselves over the surface of these muscles, but all connect anteriorly with the main thoracic air sac B while still in the meta-thorax. This is the largest air sac found in the body and runs contiguous





<sup>to</sup>  
~~with~~ the median surface of the dorso-longitudinal muscles giving off many branches to these muscles. Just below the phragma, dividing the meta- and meso-thorax, this important air sac gives off a branch, which runs transversely beneath the dorso-longitudinal muscles and forms a compound plexus (II p) receiving branches of the thoracic tracheal system at the different muscle levels, and finally connecting with the second thoracic spiracle. Anteriorly another ventral branch is given off by air sac B which joins indirectly the smaller chamber of spiracle I. This completes the dorsal thoracic tracheae shown in Fig. 1.

On the lateral surface of the dorso-longitudinal muscles two arched tracheae are found supplying air to these muscles. These are only partly shown in Plate I, Fig. 2. One of these originates at spiracle I (I-D) and connects posteriorly with air sac D, situated just anterior to the phragma dividing the meso- and meta-thorax, which in turn is joined ventrally with plexus II p. The lateral side of the longitudinal muscles of the meta-thorax is furnished by an arched tracheal tube which originates at II p (Fig. 2, II-III a) and ends at spiracle III.

Upon removing the dorso-longitudinal muscles of Fig. 1 the tracheae shown in Fig. 2 are exposed. From spiracle I two main tubes run contiguous <sup>to</sup> ~~with~~ the dorso-ventral muscles of the meso-thorax (I-II b<sub>1</sub>, I-II b<sub>2</sub>) and each terminates at the second spiracular plexus II p. A trachea II-III b, originates at II p and runs dorsalward in the meta-thorax contiguous <sup>to</sup> ~~with~~ the dorso-ventral muscles and continues over the dorsal edge of these muscles connecting with a small air sac shown in Plate I, Fig. 3, E, which in turn is indirectly united with spiracle III.





Upon removing the dorso-ventral muscles shown in Fig. 2 the more complicated tracheal system shown in Fig. 3 is exposed. In general this consists of a single principal trachea I-II c, which connects spiracle I with II p and a trachea II-III c which connects II p with spiracle III. In the meso-thorax I-II c gives off a ventral tube which connects with the tube g shown in Fig. 1. At the middle of II-III c the main meta-thoracic trachea of Fig. 2 (II-III b<sub>1</sub>) after passing through air sac E joins the tracheal system of figure 3. Ventrally II-III c gives off an air sac F which connects with the subventral trachea w of figure 1. The other trachea which is given off ventrally by II-III c supplies tracheoles to the muscles. At III (Fig. 3) is shown a tube (tc) which runs antero-ventrally and is the origin of the thoraceo-cephalic trachea (tc figure 1).

In Plate II, Figure 7 are shown the tracheae which lie just under the layer of muscles shown in Plate I, Fig. 3, but these have been drawn by removing the exoskeleton of the thorax. In Fig. 3 the second spiracular plexus continues ventrally and connects with the main spiracular trachea as shown in Plate II, Figure 7. Another branch from air sac D also connects with this main tube. The air sacs shown in Fig. 7 will not be discussed as reference to the figure will explain their significance in supplying air to the dorso-ventral muscles. From spiracle II a ventral branch is given off which soon divides sending one branch into the meso-thoracic leg (1 2) while the other branch is connected with air sac C of Fig. 1. From spiracle III a branch is sent into the hind leg (1 3) while another connects with the air sac F the other side of which has been shown in Fig. 3. From the smaller chamber of spiracle I a trachea is given off which runs to the proleg and another main branch which runs to





the super-ventral trachea I-II b3 (Plate I, Fig. 1). The main spiracular trachea also runs dorsally giving off a branch which gives rise to the tracheae of each muscle layer.

Ventral Thoracic Tracheae. Thus far only the dorsal thoracic tracheae have been considered but all the important points connecting these two systems have been noted.

The main tube running antero-ventrally from spiracle III (Plate I, Fig. 3, tc) and continuing forward through the thorax (Fig. 1, tc) to the head is the thoraco-cephalic trachea. This tube runs each side of the ventral nerve cord to which it gives off many branches. A super-ventral branch (I-II b3 Fig. 1) arising from spiracle I runs posteriorly giving off a branch which forms an air sac C (Fig. 1) which in turn is almost directly connected with spiracle II (see Plate II, Fig. 7 & Plate I, Fig. 3). Near this air sac another branch is given off (Fig. 1, g) which connects with the ventral meso-thoracic trachea given off by I-II c of Fig. 3. Other branches of this trachea run into the meta-thoracic muscles where they repeatedly divide, while the main tube (II-13) continues on and enters the metathoracic leg. An anterior branch is given off near air sac C which supplies air to the salivary glands located in the meso-thorax. An air tube w (Fig. 1) which arises from the lateral spiracular trachea of the abdomen between spiracle III and IV runs forward and joins with air sac F (Plate I, Fig. 3).





### c. Abdominal Tracheal System

In comparison with the cephalic and thoracic tracheal system that of the abdomen is simple. From each abdominal spiracle short air tubes connect with a main longitudinal spiracular trachea (spt, Fig. 8 & Fig. 9) which extends from spiracle X forward on each side of the abdomen to spiracle III. From this spiracular trachea originate all the branches found in the abdomen. Typically in each segment of the abdomen bearing a spiracle three main tubes are given off by the spiracular trachea of that segment. One runs dorsally to connect with an undulating longitudinal dorsal trachea and soon after leaving the spiracular trachea gives off a branch which becomes distended forming a large air sac which is connected with the air sac of both the preceding and following segments. A ventral branch is also given off by the main spiracular trachea which unites with the ventral tracheal system. In addition to the dorsal and ventral branches a median tube is given off which supplies the alimentary canal with its tracheae.

In describing the abdominal tracheal system three main divisions are recognized: (1) Dorsal, (2) Ventral, and (3) Alimentary tracheae.

Dorsal Abdominal Tracheae (Plate II, Fig. 8). In each segment of the abdomen bearing a spiracle, a dorsal branch, the dorso-segmental trachea, is given off by the main spiracular trachea. These branches connect dorsally with a right and left dorso-abdominal trachea (da) which runs in close approximation to the alary muscles of the heart. The dorso-abdominal trachea extends from spiracle III to beyond spiracle X, the latter spiracle being connected with this tube by three dorso-segmental tracheae instead of one. The right and left dorso-abdominal trachea are independent and are in no way connected by transverse tubes.





The abdominal air sacs are closely associated with both the dorsal and alimentary tracheal systems. There are eight of these sacs on each side which originate as branches of the dorso-segmental tracheae and those of each side are all connected by a longitudinal trachea which runs along the top of the alimentary canal and reproductive organs. These are usually found imbedded in the fat body. Over the ileum in the sixth abdominal segment the right and left longitudinal tracheae connecting the air sacs unite to form the ileal plexus (Ip). The air sacs arising from spiracles IX and X join directly with this plexus as shown in figure 8.

Ventral Abdominal Tracheae (Plate II, Fig. 8 and 9). In the dorsal abdominal tracheal system the two dorso-abdominal tracheae run contiguous <sup>to</sup> ~~with~~ the alary muscles of the heart but are in no way connected with each other. In the ventral system a single ventro-segmental tube is given off by the spiracular trachea in every segment bearing a spiracle. This segmental tube runs ventrally to join a ventro-abdominal trachea (va) situated on each side of the nerve cord in every segment bearing a spiracle. Instead of the right and left ventro-abdominal trachea being separate they are joined by a transverse tube which runs beneath the nervous system. This ventral system gives off many branches to the nerve cord and at its posterior extremity these tracheae give rise to branches which supply the genital organs (x). Anteriorly this system ends in small air sacs situated in the first abdominal segment.





Alimentary Canal Tracheal System (Plate 3, Fig. 16) With the exception of a short branch of I 2b<sup>u</sup> (Plate 1, Fig. 1) which is contiguous to the proventriculus all of the tracheal tubes connecting with the alimentary canal arise from the abdominal spiracles. From spiracle 3 two air tubes run to the alimentary canal, one connecting with the lateral alimentary trachea (lr), the other connecting with the superior alimentary trachea (sp). These longitudinal tubes, the lateral and superior alimentary tracheae, are situated between the coecal pouches and are continued posteriorly in a more or less indefinite manner until opposite spiracle 8, where they unite to form a single tube which connects with spiracle 10. The superior alimentary trachea gives off many branches between its connections with spiracle 6 and 8, which enter the reproductive organ. The two branches given off by spiracle 3 supply the dorsal and lateral sides of the alimentary canal in the vicinity of the coecae, while the single branch given off from spiracle 4 supplies only the ventral portion of this region. From spiracles 5, 6, 7, and 8, two branches are sent to the alimentary canal, one, a dorsal tube connecting with the superior alimentary trachea (sp), the other a ventral branch supplying the ventral side of this canal. Spiracle 9 furnishes a ventral tube running beneath the ileum, and a dorsal dilated tube which connects with the ileal plexus (Ip). From spiracle 10 many branches arise which supply tracheae to the digestive canal and to the muscles of the reproductive organs. The most important trachea given off by this spiracle is a dilated tube which connects with the ileal plexus (Ip).

In Plate III Figure 16 the alimentary tracheal system has only been drawn for the left side. On the right side the air sacs which occur in the abdomen have been figured. These are also shown in Plate II, Fig. 8.





The air sacs on each side of the abdomen are connected by a longitudinal tube which joins posteriorly the ileal plexus (Ip). This plexus, then, consists of six more or less dilated tubes which unite just anterior to the rectum and above the ileum.

In figure 16 only the right half of the rectum has been drawn in order that the origin of the tracheae which appear on it may be better shown on the left side.



Terminology.

Spiracle Terminology.

I-- First thoracic spiracle.

II-- Second thoracic spiracle.

III-- First abdominal spiracle.

IV to X-- Second to eighth abdominal spiracles.

stm-- Septum.

ocm-- Occluding muscle.

In Figure 16 Arabic numerals (3 to 10) are used instead of Roman numerals to represent the spiracles.

Tracheal Terminology.

Air sacs.

A-- Cephalic air sac.

B-- Main thoracic air sac.

C-- Air sac connecting with spiracle II.

D, E, & F-- Other air sacs found in thorax.

Tracheal Tubes.

(a) Head.

I<sub>1</sub>-- Superior cephalic trachea.

I<sub>2</sub> (a & b)-- Median cephalic trachea and branches.

gt-- Genal trachea.

ot-- Ophthalmic trachea.

tc-- Thoraco-cephalic trachea.

Tp-- Anterior tentorial arm plexus.





(b) Thorax.

alc-- Trachea to alimentary canal.

g-- " connecting with I--IIc (Fig.3).

$l_1, l_2, l_3$ -- pro-, meso-, and metathoracic leg trachea.

IIP-- Second spiracular plexus.

tc-- Thoraco-cephalic trachea.

w-- Trachea connecting with air sac F.

Tracheae found between the thoracic muscles are designated by combining two Roman numerals. I--IIb = a trachea connecting spiracle I with spiracle II. The letters a, b, and c, denote the muscular layer in which these tubes appear. Fig. 1 = layer a; Fig. 2 = layer b; Fig. 3 = layer c.

(c) Abdomen.

da-- Dorso-abdominal trachea.

Ip-- Ileal plexus.

lr-- Lateral alimentary trachea.

sp-- Superior alimentary trachea.

spt-- Spiracular trachea.

va-- Ventro-abdominal trachea.

x (Fig.9)-- Trachea supplying air to reproductive organs.

I--X or 3--10-- See Spiracle Terminology.



Explanation of Plates.

Plate I.

- Figure 1-- Median sagittal section of head and thorax.
- Figure 2-- Longitudinal dorsal muscles of the thorax removed from Figure 1 to show the dorsal tracheae lying beneath.
- Figure 3-- Muscular layer shown in Figure 2 removed to show the tracheae and muscles in the next layer. This is an internal view of the lateral thoracic muscles.
- Figure 4-- Situation of the spiracles.
- Figure 5-- Side view of head showing tracheae.
- Figure 6-- Front view of head showing tracheae.

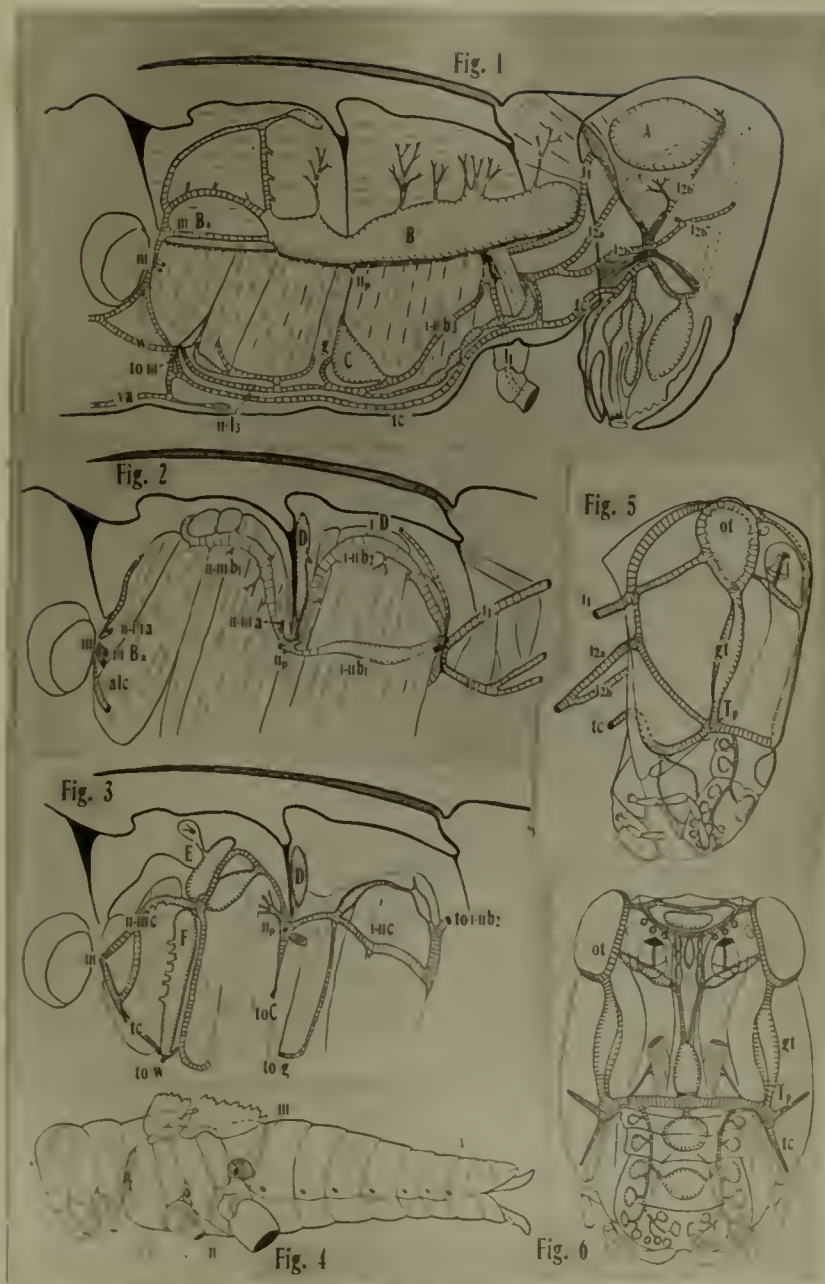
Plate II.

- Figure 7-- External view of lateral muscles shown in Figure 3.
- Figure 8-- Sagittal section of the abdomen with the digestive canal removed to show the abdominal air sacs, dorsal and ventral tracheal systems together with the spiracular trachea.
- Figure 9-- Ventral abdominal tracheal system.
- Figure 10-- Dorsal aspect of head showing tracheae of this region.
- Figure 11-- Internal view of the first thoracic spiracle situated on the right side of the body.





# Plate I





# Plate II



Fig. 7



Fig. 11



Fig. 8



Fig. 12

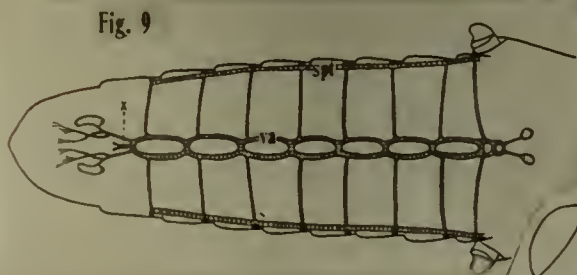


Fig. 9

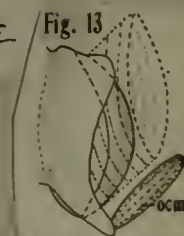


Fig. 13

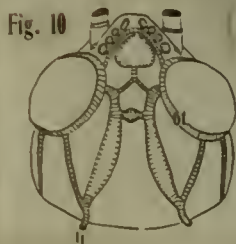


Fig. 10

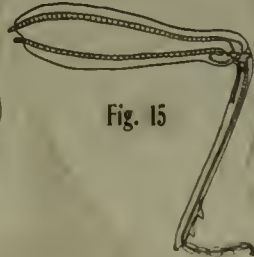


Fig. 15

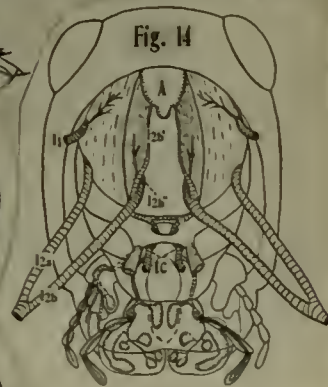


Fig. 14





Plate III

